PAN-PACIFIC ENTOMOLOGIST
65(1), 1989, pp. 50–57

Observations on the Host Spectrum of the California Oakworm, *Phryganidia californica* Packard (Lepidoptera: Dioptidae)

JAMES E. MILSTEAD

Division of Entomology and Parasitology, University of California, Berkeley, California 94720.

The California oakworm, *Phryganidia californica* Packard, is a herbivore commonly found on coast live oak in the San Francisco Bay Area. The larvae are reported to occasionally overwinter on deciduous oaks (Burke, 1919) but the species appears to require evergreen foliage in order to maintain spatial and temporal continuity within the boundary limits of its potential hosts.

The host spectrum of the California oakworm appears to consist primarily of members of the family Fagaceae. Kellogg and Jack (1895) recognized 5 native species of oaks: *Quercus agrifolia, Q. lobata, Q. kelloggii, Q. dumosa* and *Q. douglasii* that could serve as hosts. This list was subsequently expanded to include *Q. chrysolepis* (Kellogg, 1908), *Q. suber* (Essig, 1915), *Castanea dentata* and *Eucalyptus globulus* (Burke and Herbert, 1920), *Q. tomentella, Q. bicolor, Q. rubra, Q. robur, Lithocarpus densiflora, Carya ovata, C. tomentosa, Castanea sativa, Betula papyifera* (Sibray, 1947), *Q. durata* (Harville, 1955), *Q. velutina, Q. virginiana* (Tietz, 1972), *Rhododendron occidentale* (Furniss and Carolin, 1977) and *Castenopsis chrysophylla* (Wickman and Kline, 1985).

While it is generally held that all native and introduced oaks can support oakworm development, temporary feeding on unrelated native and exotic species (here termed incidental hosts) may occur during periods of high population density when preferred foliage has been depleted (Sibray, 1947) and larval starvation is imminent. Cursory observation of such behavior may lead to unwarranted assumptions of nutritional adequacy for these incidental hosts which are never subsequently tested by controlled rearing studies.

More than 150 species including native flora associated with oaks as well as fruit trees and ornamentals have been tested on newly hatched and nearly mature larvae (Sibray, 1947) with generally negative results. Unfortunately this author failed to provide a complete list of species tested so that it is impossible to verify many of his findings.

The current study reports on rearing trials conducted between 1983 and 1987 on native and exotic oaks as well as other oak associates located primarily on the University of California Campus at Berkeley.

MATERIALS AND METHODS

Two types of rearing trials were conducted: 1) in which a single host species was utilized throughout the entire larval period and 2) in which outbreak conditions were simulated and last instar larvae were transferred from *Q. agrifolia* leaves to leaves of other species (terminal hosts).

All larvae were maintained at 20°C in 13-dram plastic vials and fed mature

Table 1. Influence of incidental host plants on survival of first-instar larvae of the California oakworm.

Host	No. of trials	Month foliage sampled	n larvae tested	Age at 100% mortality[1] (days) ($\bar{x} \pm$ SE/trial)
Alnus rhombifolia	5	March	144	8.0 ± 1.5
Arbutus menziesii	5	Aug., Sept.	222	5.2 ± 1.0
Arctostaphylos columbiana	1	Apr.	31	10.0 ± 0
Betula papyifera	13	March, Apr., May	724	34.4 ± 4.6
Eucalyptus globulus	5	May	53	4.6 ± 0.4
Fagus grandiflora	1	Sept.	4	14.0 ± 0
Fagus sylvatica	1	Sept.	4	34.0 ± 0
Garrya eliptica	7	Jan., Aug.	143	7.6 ± 1.4
Heteromeles arbutifolia	1	Mar.	18	6.0 ± 0
Liquidambar styraciflua	9	Mar.	317	7.8 ± 0.8
Ulmus americana	2	Apr., May	162	24.0 ± 14.0
Ulmus procera	5	Oct.	145	14.8 ± 1.8
Starvation	10		328	6.0 ± 0.3

[1] No larvae survived beyond the second instar.

excised leaves selected from the lower crown area of the same donor trees. Foliage was replaced 3 times per week. No attempt was made to control or monitor the relative humidity. The initial number of larvae was determined by the egg mass size and all larvae were reared individually after the first instar.

Feeding arenas were examined daily and mortalities recorded. Insects were weighed at the onset of pupation and adult eclosion.

Matings were carried out in plastic vial arenas. *Q. agrifolia* leaves were replaced 3 times per week to provide a fresh ovipositional substrate.

Leaf moisture was estimated by comparing initial weights of fresh leaves with weights obtained after a 24 hr ovenization at 105°C (Volney et al., 1983).

Table 2. Influence of native and exotic fagaceous host plants on the survival of California oakworm larvae.

Host species	No. of insects reared	% survival to adult
Quercus agrifolia	273	42
Q. chrysolepis	70	23
Q. douglasii	92	57
Q. englemanii	5	40
Q. kelloggii	30	30
Q. lobata	74	60
Q. alba	21	48
Q. cerris	5	60
Q. ilex	14	36
Q. macrocarpa	86	49
Q. mongolica	81	56
Q. phellos	29	59
Q. robur	4	25
Q. rubra	4	25
Castenopsis sempervirens	15	20
Lithocarpus densiflora	46	15

Table 3. Influence of native and exotic fagaceous hosts on developmental rate, size and fecundity of California oakworm.

Treatment	Host species	Duration of larval period (days) ($\bar{x} \pm$ SE)				Pupal weight (mg) ($\bar{x} \pm$ SE)	
		n	♀	*n*	♂	*n*	♀
1	*Q. agrifolia*	61	54.1 ± 2.8	53	45.7 ± 2.8	60	110.0 ± 4.9
2	*Q. chrysolepis*	10	65.4 ± 7.4	6	52.2 ± 2.1	10	86.8 ± 9.4
3	*Q. douglasii*	25	50.9 ± 1.1	28	52.5 ± 2.4	24	104.3 ± 3.3
4	*Q. kelloggii*	4	44.3 ± 0.5	5	55.8 ± 6.3	4	149.8 ± 23.1
5	*Q. lobata*	30	47.0 ± 1.1	16	38.7 ± 0.7	30	132.3 ± 5.9
6	*Q. macrocarpa*	22	45.0 ± 1.0	21	36.8 ± 0.8	22	163.2 ± 5.0
7	*Q. mongolica*	20	47.6 ± 3.5	22	49.1 ± 5.9	18	138.7 ± 9.0
	Native species	$F = 2.73$, $P = 0.05$		$F = 2.53$, $P = 0.05$		$F = 5.82$, $P = 0.01$	
	All species	$F = 2.97$, $P = 0.01$		$F = 2.72$, $P = 0.05$		$F = 17.77$, $P = 0.01$	
Paired contrasts significant at:							
$P = 0.05$		2 vs. 7		1,7 vs. 6		1 vs. 4; 2 vs. 3	
$P = 0.01$		2 vs. 3				1 vs. 5,7; 2 vs. 4	
$P = 0.001$		2 vs. 5,6; 3 vs. 6		2,3,4 vs. 5,6		2,3 vs. 5; 3 vs. 4; 1,2,3,5 vs. 6; 2,3,6 vs. 7	

Table 3. Continued.

Treatment	Pupal weight (mg) ($\bar{x}$ ± SE)		Adult weight (mg) ($\bar{x}$ ± SE)				Eggs laid ($\bar{x}$ ± SE)	
	n	♂	*n*	♀	*n*	♂	*n*	Total
1	51	71.4 ± 4.9	51	92.4 ± 4.7	52	34.5 ± 1.6	52	98.6 ± 7.5
2	6	56.0 ± 6.1	9	67.2 ± 9.5	6	25.8 ± 2.8	8	79.1 ± 20.2
3	27	70.9 ± 2.1	26	79.2 ± 2.8	27	32.5 ± 1.9	15	90.5 ± 8.6
4	5	60.7 ± 7.9	3	109.6 ± 23.3	4	44.2 ± 8.5	2	179.5 ± 17.5
5	16	87.4 ± 3.7	29	104.5 ± 5.3	15	46.4 ± 5.2	19	122.9 ± 10.8
6	21	99.8 ± 3.3	19	128.3 ± 4.8	21	50.4 ± 4.1	18	156.4 ± 13.5
7	18	80.8 ± 3.5	18	115.0 ± 9.6	17	44.2 ± 2.9	15	163.9 ± 27.8
	$F = 6.33$, $P = 0.01$		$F = 4.52$, $P = 0.01$		$F = 4.58$, $P = 0.01$		$F = 2.71$, $P = 0.05$	
	$F = 13.93$, $P = 0.01$		$F = 8.22$, $P = 0.01$		$F = 6.51$, $P = 0.01$		$F = 4.98$, $P = 0.01$	
Paired contrasts significant at:								
$P = 0.05$	1 vs. 2; 1,3,4 vs. 7; 5 vs. 6		1 vs. 2,7		2 vs. 4,5		1,2 vs. 4; 3 vs. 7; 2,3 vs. 5	
$P = 0.01$	1,4 vs. 5; 2 vs. 3,6		2 vs. 5,7; 5 vs. 6		1,3 vs. 5; 2 vs. 6; 1,2,3 vs. 7		1 vs. 7; 2 vs. 6; 3 vs. 4	
$P = 0.001$	2,3 vs. 5; 1,2,3,4,7 vs. 6		1,2 vs. 6; 3 vs. 4,5,6,7		1 vs. 6		1,3 vs. 6	

Table 4. Influence of terminal host plants on survival, larval longevity and duration of larval period of last instar larvae of the California oakworm.

Treat-ment	Host species	No. leaves assayed	% moisture ($\bar{x} \pm$ SE)	No. larvae tested	% survival	Larval longevity (days) ($\bar{x} \pm$ SE)	Duration of larval period (days) ($\bar{x} \pm$ SE)			
							n	♀	*n*	♂
1	*Arctostaphylos columbiana*	20	52.0 ± 0.2	32	0	9.5 ± 0.2				
2	*Betula papyifera*			21	14.3	18.1 ± 2.2	1	24.0 ± 0	5	22.4 ± 4.8
3	*Eucalyptus pulverulenta*	20	49.1 ± 0.3	33	0	10.8 ± 0.3				
4	*Garrya eliptica*	20	48.6 ± 0.6	31	0	9.9 ± 0.4				
5	*Heteromeles arbutifolia*	18	48.1 ± 0.3	55	1.8	11.6 ± 0.6				
6	*Lithocarpus densiflora*	20	46.5 ± 0.4	35	88.6		12	18.5 ± 0.8	20	14.9 ± 0.5
7	*Quercus agrifolia*	20	49.9 ± 0.3	88	92.0		25	17.2 ± 0.7	56	13.3 ± 0.3
8	*Umbellularia californica*	20	52.9 ± 0.3	27	0	11.1 ± 0.7				
9	Starvation			16	0	9.9 ± 0.3				
			$F = 38.06$, $P = 0.01$			$F = 67.0$, $P = 0.01$	$F = 9.89$, $P = 0.01$		$F = 19.9$, $P = 0.01$	
Paired contrasts significant at:										
$P = 0.05$			1 vs. 8; 3 vs. 5			1 vs. 8; 4 vs. 5				
$P = 0.01$			4 vs. 6			1 vs. 3,5; 2 vs. 8,9			6 vs. 2,7	
$P = 0.001$			1,8 vs. all; 6 vs. 3,5,7; 5 vs. 7			2 vs. 1,3,4,5			2 vs. 7	

Data were analyzed using an analysis of variance. Means were compared using the method of least significant difference.

Results

The results of a series of feeding trials in which attempts were made to rear first-instar larvae on incidental hosts are presented in Table 1. Only *Betula, Fagus* and *Ulmus* supported survival for as long as 2 wk and no larval development to the third instar was observed. Negative results were also obtained with the fall foliage of *Corylus cornuta* var. *californica* and *Ribes divaricatum.* These disparities in larval performance are not attributable to leaf age.

Similar trials were conducted using foliage taken from native and exotic oaks, tanbark and chinkapin. The results of these trials (Table 2) contrast sharply with those of Table 1. Only *Q. niger* and *Q. laurifolia* failed to support development to the adult stage and with both species, feeding and frass production was observed.

During the late summer flight period of 1986, male moths were observed hovering about the canopies of all of these native and exotic species on the Berkeley Campus with the single exception of *Q. mongolica.* Oviposition and larval feeding was also observed in the Tilden Park Botanical Garden, Berkeley, California on *Q. agrifolia, Q. chrysolepis, Q. dumosa, Q. durata, Q. douglasii, Q. dunni, Q. garryana, Q. garryana* var. *semota, Q. kelloggii, Q. lobata, Q. ×macdonaldi, Q. parvula, Q. saddleriana, Q. tomentella, Q. turbinella* var. *turbinella, Q. turbinella* var. *californica* and *Q. wislizenii.*

Extensive defoliation also occurred on *Q. agrifolia, Q. chrysolepis* and chinkapin in the Huckleberry preserve, Oakland, California.

In addition oakworm were observed to feed on *Q. turbinella* foliage collected from the Mohave Desert near Chloride, Arizona and the insects were reared to adulthood on foliage of *Q. gambelii* (collected from the Mingus Mountains, Prescott, AZ) and *Q. vaccinifolia* (collected from Echo Lake, El Dorado, CO).

The influence of foliage sampled from *Lithocarpus densiflora* and *Quercus* species on developmental rate, insect mass and fecundity is presented in Table 3. Ratios of pupal wet weight to the duration of the larval period (pw/t) show that growth rates for females are greater than that for males on comparable foliage. The highest values for female larvae occurred on the deciduous species *Q. macrocarpa, Q. kelloggii, Q. lobata* and *Q. mongolica.* Feeding trials with the latter species using small immature leaves, however, consistently resulted in 100% mortality. Ratios of realized fecundity to pupal weight paralleled pw/t values. The poorest performance occurred on *Q. chrysolepis* and *Q. douglasii.*

Tables 4 and 5 present data derived from experiments in which larvae reared during the early instars on *Q. agrifolia* foliage were transferred at the onset of the last instar to foliage of a terminal host.

Table 4 compares the influence of coast live oak and tan oak with native and exotic incidental hosts on larval/pupal survival, larval longevity and duration of the larval period. European birch proved clearly superior to the other incidental hosts tested in supporting development. However, in contrast with *Quercus agrifolia* and *Lithocarpus,* larvae reared on *Betula* suffered a much higher mortality, required a longer larval period to reach pupation and produced smaller pupae and adults with greatly reduced fecundity (Table 5). A single male survivor on *Heteromeles* weighed only 6 mg and probably would have been incapable of mating.

Table 5. Influence of terminal host plant on pupal weight, adult weight and fecundity of California oakworm.

Treatment	Host species	Pupal weight (mg) ($\bar{x} \pm$ SE)			
		n	♀	n	♂
1	*Betula papyifera*	1	72.6 ± 0	5	47.5 ± 4.6
2	*Lithocarpus densiflora*	12	108.6 ± 9.3	20	75.2 ± 2.9
3	*Quercus agrifolia*	25	137.4 ± 6.4	56	81.4 ± 13.9
		$F = 4.72, P = 0.05$		$F = 14.63, P = 0.01$	
Paired contrasts significant at:					
$P = 0.05$		2 vs. 3		1 vs. 3	
$P = 0.01$				2 vs. 3	

Discussion

Although *Phryganidia californica* is not strictly monophagous (Puttick, 1986) it does appear to generally restrict itself to fagaceous hosts.

The inability of most native and exotic incidental hosts to support feeding and development of first-instar larvae precludes the possibility of such species playing a direct role in oakworm population dynamics since the insect overwinters at this stage in its life cycle. These plants, however, may provide allomonal protection to later larval and pupal stages from natural enemies.

While the population density of *Phryganidia* is generally sparse, heavy infestations periodically result in severe defoliation to fagaceous hosts and under such circumstances oakworm larvae may be observed crawling and feeding on nearby plant associates.

These species can be termed true hosts if larval feeding results in the production of robust adults capable of mating and producing viable offspring.

Of the nonfagaceous terminal hosts studied, only *Betula papyifera,* a species limited to ornamental plantings, would marginally qualify for inclusion as a host. It is possible that a related species *B. occidentalis,* which may be sympatric with California oakworm populations reported from Siskiyou County, California (Miller, 1987) could augment larval feeding in streamside habitats.

Scriber and Slansky (1981) have shown that relative larval growth rate is a function of leaf water content. This relationship does not serve to explain the disparity between *Lithocarpus* and *Arctostaphylos, Eucalyptus, Heteromeles* or *Umbellularia* and there may be allomonal factors present in the foliage of these species that act as feeding deterrents for oakworm larvae.

In a comparison of native oak species, Puttick (1986) has reported that *Q. lobata* was a better quality food source for California oakworm larvae than *Q. agrifolia.* Larvae reared on *Q. lobata* had greater efficiencies of conversion of ingested and digested food which led to more rapid larval development, greater pupal mass and enhanced fecundity. These findings are supported by the results of this study. Her generalization that deciduous oaks are a better food source than evergreen oaks is partially supported by evidence indicating that larval performance and adult fecundity was highest on *Q. kelloggii* and *Q. lobata* and lowest on *Q. chrysolepis.* However, current data suggest that the foliage of coast live and blue oak are essentially equivalent in their effects. Since the mean duration of the larval period ranged between 2 and 3 wk for both males and females it is possible that

Table 5. Continued.

Adult weight (mg) ($\bar{x}$ ± SE)				Eggs ($\bar{x}$ ± SE)	
n	♀	*n*	♂	*n*	Total
1	48.2 ± 0	2	26.5 ± 4.5	1	38.0 ± 0
12	89.0 ± 8.3	19	42.5 ± 2.5	9	114.0 ± 18.6
25	115.8 ± 5.3	56	44.5 ± 1.8	22	160.5 ± 11.4
$F = 4.65$, $P = 0.05$		$F = 1.98$		$F = 4.31$, $P = 0.05$	
1,2 vs. 3				1 vs. 2,3	

reports of the occurrence of three oakworm generations per year in the San Francisco Bay Area may be partially attributable to host mediated differences in larval developmental rate.

Because information is not yet available on the spatial and temporal variability of host metabolites and the possible influence of prior herbivory on the allocation of these metabolites quantitative differences in host nutritional suitability can at best be only rough approximations.

Results from the current study suggest that all *Quercus* species, *Lithocarpus densiflora, Castenopsis chrysophylla* and *C. sempervirens* qualify as true host species whose foliage can support larval development in areas where temperature and humidity regimes allow oakworm populations to persist.

Literature Cited

Burke, H. E. 1919. Notes on the California oak worm. Proc. Ent. Soc. Wash., 21:124–125.

———, and F. B. Herbert. 1920. California oak worm. Farmers Bulletin, 1076:3–11.

Essig, E. O. 1915. Injurious and beneficial insects. Supp. Bull. California State Host Comm., Vol. 4, Berkeley, California, 503 pp.

Furniss, R. L., and V. M. Carolin. 1977. Western forest insects. U.S.D.A. Forest Service Misc. Publ. 1339, Washington, D.C., 654 pp.

Harville, J. P. 1955. Ecology and population dynamics of the California oak moth *Phryganidia californica* Packard (Lepidoptera: Dioptidae). Microentomology, 20:83–166.

Kellogg, V. L. 1908. American insects, 2nd ed. Henry Holt, New York, 674 pp.

———, and F. J. Jack. 1895. The California Phryganidian (*Phryganidia californica* Pack.). Proc. Calif. Acad. Sci., Series 2, 5:562–570.

Miller, J. S. 1987. A revision of the genus *Phryganidia* Packard, with description of a new species (Lepidoptera: Dioptidae). Proc. Entomol. Soc. Wash., 89:303–321.

Puttick, G. M. 1986. Utilization of evergreen and deciduous oaks by the California oak moth *Phryganidia californica.* Oecologia (Berl.), 68:589–594.

Scriber, J. M., and F. Slansky, Jr. 1981. The nutritional ecology of immature insects. Ann. Rev. Entomol., 26:183–211.

Sibray, W. S. 1947. Bionomics of the California oak moth. M.S. thesis, Dept. of Entomology, Univ. California, Berkeley.

Tietz, H. M. 1972. An index to the described life histories, early stages and hosts of the macrolepidoptera of the continental United States and Canada, Vol. 1. Allyn Museum of Entomology, Sarasota, Florida, 536 pp.

Volney, W. J. A., J. E. Milstead, and V. R. Lewis. 1983. Effects of food quality, larval density, and photoperiod on the feeding rate of the California oakworm (Lepidoptera: Dioptidae). Environ. Entomol., 12:792–798.

Wickman, B. E., and L. N. Kline. 1985. New pacific northwest records for the California oakworm. Pan-Pacific Entomologist, 6:152.